

L.—On the Agency of Bees in the Fertilization of Papilionaceous Flowers, and on the Crossing of Kidney Beans. By CHARLES DARWIN, F.R.S.*

IN a brief notice published by me on this subject last year, I stated that bees always alight on the left wing-petal of the Scarlet Kidney Bean, and in doing so depress it; and this acts on the tubular and spiral keel-petal, which causes the pistil to protrude: on the pistil there is a brush of hairs; and by the repeated movement of the keel-petal the hairs brush the pollen beyond the anthers on to the stigmatic surface. This complex contrivance led me to suppose that bees were necessary to the fertilization of the flower: accordingly I enclosed some few flowers in bottles and under gauze; and those which were not in any way moved did not set a single pod, whereas some of those which I moved in imitation of the bees produced fine pods. But I then stated that the experiment was tried on much too small a scale to be trusted. I have this year covered up between 3 and 4 feet in length of a row of Kidney Beans, just before the flowers opened, in a tall bag of very thin net. Nothing in the appearance of the plants would lead me to suppose that this was in any way injurious to their fertilization: and I think this conclusion may be trusted; for some of the flowers which I moved in the same way as the bees do, produced pods quite as fine as could be found in the uncovered rows.

The result was that the covered-up plants had produced by August 13th only thirty-five pods, and in no one case two pods on the same stalk, whereas the adjoining uncovered rows were crowded with clusters of pods. There were many flowers still on the plants when uncovered; and it was curious to see how, in a few days afterwards, as soon as the bees had access to them, a number of pods hanging in clusters of three and four together were produced. On August 17th I again put the net on a later crop. The covered plants now produced ninety-seven pods, borne on seventy-four stalks, showing that the same stalk often produced more than one pod. This time I kept an equal length of uncovered beans ungathered; and on this length there were 292 pods, or exactly thrice as many as on the covered plants. Taking this number as the standard of comparison for the first experiment (which, however, is hardly fair, as my gardener thinks the second crop was more productive than the first), more than eight times as many pods were produced on the uncovered than on the covered rows. The Kidney Bean is largely frequented by the *Thrips*; and as I have with some other plants actually seen a *Thrips* which was dusted with pollen leave several granules on the

* Extracted from the 'Gardeners' Chronicle' of November 13, 1858.

stigma, it is quite possible that the fertilization of the covered-up flowers might have been thus aided.

In the common Bean there is no such obvious relation between the structure of the flower and the visits of bees; yet, when these insects alight on the wing-petals, they cause the rectangularly bent pistil and the pollen to protrude through the slit in the keel-petal. I was led to try the effect of covering them up, from a statement in the 'Gardeners' Chronicle' made several years ago, viz. that when bees bite holes through the calyx of the flower in order to get more easily at the nectar, the crop is injured. This was attributed by the writer to injury of the ovarium, which I am sure is incorrect. But I thought that it was possible that the fertilization would be less perfect, as soon as bees ceased to alight on the wing-petals. I accordingly covered up seventeen plants, just before the flowers opened, moving a few flowers to ascertain that very fine pods, including the full average number of beans, could be, and were, produced on the plants under the net. These seventeen plants produced thirty-six pods; but no less than eight of them, though well formed, did not include a single bean. The thirty-six pods together contained only forty beans, and, if the empty pods be excluded, each produced on an average less than one and a half beans; on the other hand, seventeen uncovered plants in an adjoining row which were visited by the bees produced forty-five pods, all including beans, 135 in number, or on an average exactly three beans to each pod,—so that the uncovered beans were nearly thrice as fertile as the covered.

In an old number of the 'Gardeners' Chronicle' an extract is given from a New Zealand newspaper, in which much surprise is expressed that the introduced Clover never seeded freely until the hive-bee was introduced. This statement may be erroneous; at least, as I shall immediately show, it does not apply to the Canterbury Settlement. But I was induced by it to cover up under the same open sort of net about a yard square of the common White Clover, growing thickly in turf; and I then gathered an equal number of heads from the covered and from some uncovered plants which were growing all round, and which I had seen daily visited by my bees. I collected the seed into a small parcel; and, as far as I could estimate, the uncovered plants produced just ten times as much seed as the covered. Speaking loosely, the covered heads might have been said to have produced no seed.

Lathyrus grandiflorus is very rarely visited by bees in this country; and from experiments which I have tried during the last two summers, and from experiments recorded in 'Loudon's Magazine,' I am convinced that moving the flowers favours their

fertilization, even when the young pod falls off, as very often happens almost immediately. Sir W. Macarthur, who did not know of my experiments, told me that he had found that in New South Wales the introduced *Erythrina* did not set its pods well unless the flowers were moved. From the statement in regard to the Clover in New Zealand, I wrote to Mr. Swale, of Christchurch in New Zealand, and asked him whether Leguminous plants seeded there freely before the hive-bee was introduced; and he, in the most obliging manner, has sent me a list of twenty-four plants of this order which seeded abundantly before bees were introduced. And as he states that there is no indigenous bee (perhaps this statement applies to bees resembling hive or humble bees, for some other genera are known to inhabit New Zealand), the fact that these plants seeded freely at first appears quite fatal to my doctrine. But Mr. Swale adds that he believes that three species of a wasp-like insect performed the part of bees, before the introduction of the latter: unfortunately he does not expressly state that he has seen them sucking the flower. He further adds a remarkable statement, that there are two or three kinds of grasshoppers which frequent flowers; and he says he has repeatedly watched them "release the stamens from the keel-petal,"—so that, extraordinary as the fact is, it would appear that grasshoppers, though having a mouth so differently constructed, in New Zealand have to a certain extent the habits of bees. Mr. Swale further adds that the garden varieties of the Lupine seed less freely than any other leguminous plant in New Zealand; and he says, "I have for amusement during the summer released the stamens with a pin; and a pod of seed has always rewarded me for my trouble, and the adjoining flowers not so served have all proved blind." The case of the Lupine in New Zealand not seeding freely now that bees have been introduced may be accounted for by the fact, if I dare trust my memory, that in England this plant is visited by humble-bees, and not by hive-bees.

These several facts, and the foregoing experiments, seem to me rather curious; for who, seeing that papilionaceous flowers are hermaphrodite, have an abundant supply of pollen, which is mature before the flower opens, and that the flower itself is so neatly closed, would have imagined that insects played so important a part in their fertilization? I can hardly doubt that in England, during a season when bees were very scanty, if in any one district large crops of seed-clover were planted, the crop would partly fail, from the flowers not being sufficiently moved.

The foregoing little experiments, however, were not tried in relation to the agency of insects in fertilizing a plant with its own pollen. Andrew Knight many years ago propounded the

doctrine that no plant self-fertilizes itself for a perpetuity of generations. After pretty close investigation of the subject, I am strongly inclined to believe that this is a law of nature throughout the vegetable and animal kingdoms. I am well aware that there are several cases of difficulty.

The Leguminosæ with papilionaceous flowers have been advanced by Pallas and others as a case in which crossing could never naturally take place. But any plant habitually visited by insects in such a manner that their hairy bodies, to which pollen so readily adheres, come into contact with the stigma, could hardly fail occasionally to receive the pollen from another individual of the same species. In all Leguminosæ, bees do brush over the stigma. And the possibility of crossing would be very strong in the case of any plant, if the agency of insects were necessary for its self-fertilization; for it would show that it was habitually visited by them.

From these considerations I was led to believe that papilionaceous plants must be occasionally crossed. Nevertheless I must confess that, from such evidence as I have been able to acquire, crossing between varieties growing close together does not take place nearly so freely as I should have expected. As far as I am aware, only three or four cases of such crosses are on record. It is not by any means, I believe, a common practice with seed-raisers to keep the crops of their leguminous plants separate. Hence I was led last year, in my short communication to the 'Gardeners' Chronicle,' to ask whether any of your readers had any experience on the natural crossing of Beans, Peas, &c. Mr. Coe, of Knowle, near Farcham, Hants, in the most obliging manner sent me some specimens, and an account that last summer he had planted four rows of the Negro Dwarf Kidney Bean between some rows of the white and brown dwarfs, and likewise near some Scarlet Runners. The dwarfs he had saved for seed. The plants themselves he believes presented nothing remarkable in foliage, height, flowers, &c.; and he feels sure that their pods were all alike: but the beans themselves presented an extraordinary mixture, as I can testify from the sample sent me, of all shades between light brown and black, and a few mottled with white; not one-fifth of the beans, perhaps much less, were pure Negroes. Some few of the beans also in the rows of the white Haricot were affected, but none of the brown dwarfs.

Hence, then, we apparently have the extraordinary fact, described by Wiegmann in the case of several leguminous plants experimented on most carefully by Gärtner in the case of the Pea, and described a few years ago by Mr. Berkeley in the 'Gardeners' Chronicle,' of the pollen of one variety having affected not only the embryo but the tunics of the seed borne by the pure

mother. I have said that apparently we have here a fact of this nature; for I must state that Mr. Coe sent me a dozen of the pure Negro Beans which produced in 1857 the extraordinary mixture. I sowed them this year; and though quite like each other in appearance, the dozen produced plants differing in colour of flower, &c., and beans of various tints; so that these beans, though not affected in their outer tunics, seem to have been the product of a cross in the previous year of 1856.

This year I sowed the extraordinary mixture raised by Mr. Coe in 1857 from the four rows of the Negro Bean, which he believes to have been quite pure; and the produce is the most extraordinarily heterogeneous mixture which can be conceived—each plant differing from the others in tallness, foliage, colour, and size of flower, time of ripening and flowering, size, shape, and colour of pods, and beans of every conceivable tint from black to pale brown, some dark purple and some slightly mottled, and of various sizes and shapes. My gardener remarked, as did Mr. Coe with respect to some of his plants, that some of the seedlings seemed to have been crossed by the Scarlet Runner: one of my plants trailed on the ground for a length of 4 feet, its flowers were white, and its pods were very long, flat, and broad; the beans were pinkish purple, and twice as large as those of the Negro; there were also in two cases brown and purple beans in the same pod. These facts certainly seem to indicate a cross from the Scarlet Runner; but as the latter is generally esteemed a distinct species, I feel very doubtful on this head; and we should remember that it is well established that mongrels frequently, or even generally, are much more vigorous than either of their parents.

Mr. Coe tried the experiment more philosophically, and separated his heterogeneous Negro beans into twelve lots, according to their tints; and keeping a few of each as a sample, he sowed them, and he has now harvested them separately. He has kindly sent me samples of all. The variation is now much greater than it was in the parent lot of 1857. Beans of new colours have appeared, such as pure white, bright purple, yellow; and many are much mottled. Not one of the twelve lots has transmitted its own tint to all the beans produced by it; nevertheless the dark beans have clearly produced a greater number of dark, and the light-coloured beans a greater number of light colour. The mottling seems to have been strongly inherited, but always increased. To give one case of the greatest variability, a dirty-brown bean, nearly intermediate in tint between the darkest and lightest, produced a sample which I have been enabled to divide into no less than a dozen different tints, viz. pure white, black, purple, yellow, and eight other tints between brown, slate, yellow, purple,

or black. It has been stated that a few of the white Haricots in the rows adjoining the Negroes were in 1857 slightly affected. Mr. Coe sowed some which were of a very pale brown, or cream-coloured; and he has sent me a pod produced this autumn, which pod includes two beans of the above tint and one of a pale, dirty, purplish brown.

Now it may be asked, are we justified in attributing this extraordinary amount of variation to crossing, whether or not the crossing was all confined to the year 1857? or may not the case be one of simple variation? I think we must reject the latter alternative. For, in the first place, the Negro Bean is an old variety, and is reputed to be very true; in the second place, I do not believe any case is on record of a vast number of plants of the same variety all sporting at the very same period. On the other hand, the Negroes having been planted between rows of white and brown beans, together with the facts which I have given on the importance of insect agency in the fertilization of the Kidney Bean, showing, as may be daily seen, how incessantly the flowers are visited by bees, strongly favour the theory of crossing. Moreover, the extraordinary increase in variability in the second generation strikingly confirms this conclusion; for extreme variability in the offspring from mongrels has been observed by all who have attended to this subject.

As seed-raisers do not usually take any precautions in separating their crops of leguminous plants, it may be asked, how are we to account for the extraordinary amount of crossing in Mr. Coe's plants in 1857, when almost every plant in the four rows of the Negro seems to have been affected? I may here add that, in an old paper in the *Journal of the Bath Agricultural Society*, there is an almost exactly parallel account of the crossing of several varieties of the common Bean throughout a whole field. Insect agency is always at work: but the movement of the corolla will generally tend merely to push the flower's own pollen, which is mature as soon as the flower is open, on to the stigmatic surface; and even if pollen is brought by the bees from another flower, the chances are in favour of pollen from the same variety being brought, where a large stock is cultivated.

I can explain Mr. Coe's case, and that in the *Bath Journal*, only on one hypothesis, viz. that from some cause the Negro Beans did not, at Knowle, in 1857, produce good pollen, or they matured it later than usual. This has been shown by Gärtner sometimes to occur, and would explain, with the aid of insect agency, the whole case. Believing, as I do, that it is a law of nature that every organic being should occasionally be crossed with a distinct individual of the same species, and seeing that the structure of papilionaceous flowers causes the plant's own

pollen to be pushed on to its own stigma, I am inclined to speculate a little further. It is, I think, well ascertained that very close interbreeding tends to produce sterility, at least amongst animals. Moreover, in plants, it has been ascertained that the male organs fail in fertility more readily than the female organs, both from hybridity and from other causes, and further, that they resume their fertility slower, when a hybrid is crossed in successive generations with either pure parent, than do the female organs. May we not then suppose, in the case of leguminous plants, after a long course of self-fertilization, that the pollen begins to fail, and then, and not till then, the plants are eagerly ready to receive pollen from some other variety? Can this be connected with the apparently short duration and constant succession of new varieties amongst our Peas, and, as is stated to be the case on the Continent, with Kidney Beans?

These speculations may be valueless; but I venture earnestly to request any of your correspondents who may have noticed any analogous facts connected with sudden and large variation in their seed-crops of any leguminous plants (including Sweet Peas), or any facts bearing on such plants having kept true for many consecutive generations when grown near each other, to have the kindness to take the trouble to communicate them to the 'Gardeners' Chronicle,' or to the following address, C. Darwin, Downe, Bromley, Kent.

II.—*Description of a new species of Bird from Palestine.*

By PHILIP LUTLEY SCLATER, M.A., F.L.S.

Amydrus Tristramii.

Saturate purpureo-nitens, ventre obscuriore; alis caudaque obscure nigris viridi-nitente marginatis: alarum primariis omnibus clare ochraceo-fulvis, nigricanti-fusco late terminatis, extimo quoque eodem colore extus partim limbato: rostro et pedibus nigris.

♀ mari similis, sed paulo minor, obscurior, et præcipue in capite et gutture fusca.

Long. tota maris 11·0, alæ 5·9, caudæ 4·5, rostri a rictu 1·4, tarsi 1·25.

Hab. in Terra Sancta.

A pair of this fine species, which belongs to the brilliant group of *Lamprotornithinæ*, or Glossy Starlings, was obtained by the Rev. H. B. Tristram in Palestine during the present spring, and I have called it after its discoverer. It forms a third of the small group to which Cabanis's term *Amydrus* is now restricted. It is rather larger than *Amydrus fulvipennis* (Sw.) of Western and Southern Africa; and the primaries are of a uniform pale buffy